HOW DOES SIMULATED GOPHER DISTURBANCE AFFECT THE ESTABLISHMENT OF *HOLCUS LANATUS* L. (POACEAE) IN CALFORNIA COASTAL PRAIRIE?

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Abstract

Disturbance often has the net effect of promoting invasive plant establishment, but the precise nature of the relationship between disturbance and invasion can depend on community context. We used simulated gopher mounds in bare and monoculture plots of three California native grasses (*Bromus carinatus* var. *maritimus* [Piper] C. L. Hitch., *Festuca rubra* L., and *Calamagrostis nutkaensis* [J. Presl] Steudel) to test the effects of mounds on seedling establishment and survival of the European perennial grass *Holcus lanatus* L. Soil disturbance treatments were crossed with manipulations of the plant canopy (shade cages in bare and *Bromus* plots vs. pinning back grass leaves in *Festuca* and *Calamagrostis* plots) to separate some of the positive and negative effects of natural mounds. Mean PAR measured in February at the soil surface varied from 11 to 969 μm/m²/s. As predicted, shade structures that decreased light availability but also increased soil moisture generally increased *Holcus* seedling establishment and survival in bare and *Bromus* plots. In contrast, *Holcus* seedling establishment increased in response to increased light availability and soil disturbance in *Festuca* and *Calamagrostis* plots, even where water availability was lower. Thus, the relative importance of light and water availability across plot types appeared to determine the effect of disturbance on invasive plant establishment. Ultimately, *Holcus* survival was low on mounds in bare plots and on unshaded mounds in *Bromus* plots, and similarly low numbers of *Holcus* seedlings survived across all treatment combinations in *Festuca* and *Calamagrostis* plots. Therefore, our results do not support the hypothesis that gopher mounds explain the invasion of *Holcus* in native-dominated coastal prairie sites.

Key Words: *Bromus*, coastal prairie, *Calamagrostis*, *Festuca*, *Holcus*, invasion.

The importance of canopy gaps to seedling establishment and species turnover in grassland vegetation has been well documented (e.g., Watt 1947; Platt 1975; Goldberg 1987; Foster et al. 2002). For example, mounds created by *Thomomys bottae* (Eydoux and Gervais 1836) (pocket gophers) are common in California grasslands and can significantly affect plant community composition (e.g., Hobbs and Mooney 1991; Stromberg and Griffin 1996). The population growth of exotic species is one type of vegetation change that frequently occurs as the result of small-scale disturbances (e.g., Foster et al. 2002; Dethier and Hacker 2005; Milbau et al. 2005). In California grasslands, gopher activity can promote the dominance of exotic annual grasses (Hobbs and Mooney 1991; Stromberg and Griffin 1996; Kotanen 1997; Seabloom et al. 2005), exotic forbs (Gerlach and Rice 2003), an invasive perennial succulent (D'Antonio 1993), and exotic perennial grasses (Peart 1989b). Yet soil disturbances do not always promote non-native species in California grasslands: the context in which disturbances occur is important

in determining whether they will be colonized by invading species (DiVittorio et al. 2007).

The net effect of a disturbance is the result of positive and negative factors affecting plant performance (Sousa 1984; Goldberg 1987; Cahill and Casper 2002). In California coastal prairie, light (Peart 1989b) and nitrogen (Kotanen 1997; Canals et al. 2003) availability are both higher on mounds than in undisturbed vegetation, and root competition is likely to be lower (Cahill and Casper 2002). Conversely, mound soils have lower bulk density and are warmer and drier than undisturbed soils (Kotanen 1997; Canals et al. 2003), which likely inhibits seedling establishment, particularly in low rainfall years. In addition, local plant composition is likely to influence the net effect of gopher mounds. For example, if a disturbance removes or reduces the cover of a competitive resident, the positive effects of disturbance likely outweigh the negative ones, thereby facilitating invasion. Conversely, tall neighbors could shade gopher mounds, reducing the harsh moisture and temperature conditions of an open mound and reinforcing the

positive effects of disturbance. Thus, to accurately predict the overall relationship between disturbance and invasibility, we must understand how the positive and negative effects of disturbance vary with the community context in which they occur.

Holcus lanatus L. (velvet grass or Yorkshire fog) is a problematic invader of California coastal prairie (Pitcher and Russo 1988) and is listed by the California Invasive Plant Council as a moderate impact invader (Cal-IPC 2013). Grime (1979) characterized *Holcus* as a ruderal-perennial herb, with a capacity for rapid spread. *Holcus* was found to be competitively dominant to three native and two other exotic perennial grasses in a greenhouse experiment (Thomsen et al. 2006a) and can produce seed in its first year of growth (Peart 1989b; Thomsen et al. 2006b). An earlier field experiment indicated that patches of the native grasses *Festuca rubra* L. and *Calamagrostis nutkaensis* (J. Presl) Steudel are highly resistant to *Holcus* invasion (Thomsen and D'Antonio 2007). In contrast, *Holcus* rapidly established in bare plots and plots dominated by the native perennial grass *Bromus carinatus* var. *maritimus* (Piper) C. Hitch. The spread of *Holcus* in native-dominated coastal prairie sites may result from its ability to enter patches dominated by less resistant species. Alternatively, we hypothesized that gopher mounds could promote *Holcus* seedling establishment by creating gaps in the cover of otherwise competitive species.

Here, we examine the interactive effects of shading and soil disturbance on the establishment and survival of *Holcus* seedlings in bare and monoculture plots in a California coastal prairie. Crossed shading and soil disturbance treatments separate some of the positive and negative effects of gopher mounds. Measurements of light, nitrogen (N), and water availability were made across treatments to gain insight as to the mechanism of the disturbance effects. Our earlier experiment indicated that high light availability is associated with invasibility in bare and *Bromus* plots, while low light availability contributed to the resistance of *Festuca* and *Calamagrostis* patches (Thomsen and D'Antonio 2007). Thus, we predicted that altered light availability would have opposite effects in these plots. Furthermore, since *Holcus* readily invades bare and *Bromus* plots in the absence of disturbance, and since *Holcus* is water-limited in some coastal prairie sites (Thomsen et al. 2006b), we predicted that the drier conditions on mounds would decrease *Holcus* performance relative to undisturbed areas of those plots, particularly when unshaded. In contrast we predicted that gopher disturbance in plots of resistant species like *Festuca* would have a net positive effect on *Holcus* establishment.

METHODS

The experiment was conducted in grassland at the University of California Bodega Marine Reserve (BMR), 80 km north of San Francisco in Sonoma County, California (38°18′N, 123°03′W). Climate at the site is typical for California coastal prairie; mean annual temperature is 12°C and mean annual rainfall is 85 cm, 83% of which falls between November and March. European annual grass species comprise much of the cover in the BMR grassland, although native perennial grass species are also common (Kolb et al. 2002). *Holcus* is of conservation concern at BMR, dominating approximately 20% of the grassland area (J. Soanes, Bodega Marine Reserve, personal communication) and forming nearly monospecific stands. *Holcus* spreads readily via decumbent tillers, forming loosely tufted patches (Thompson and Turkington 1988); plants at BMR average 30 cm in height.

Forty-four 1 m² plots were established in an area of the BMR dominated by *Holcus,* as part of the experiment described in Thomsen and D'Antonio (2007). Plots were separated by 1.5 m aisles that were mowed annually to prevent *Holcus* seed inputs. Each plot was randomly assigned to one of four "cover type" treatments: bare plots and monocultures of the three native grass species *Bromus carinatus* var. *maritimus*, *Festuca rubra*, and *Calamagrostis nutkaensis*. Species were chosen to represent the diversity of form among California native grasses, particularly variation in foliage density, phenology, and canopy height. *Bromus* individuals averaged four cm tall in experimental plots and have a sparse, prostrate growth form, while *Festuca* and *Calamagrostis* are upright bunchgrasses, averaging 30 vs. 45 cm tall (Thomsen and D'Antonio 2007). Seeds were collected at BMR (*Bromus, Calamagrostis, Holcus*) and at a nearby coastal prairie remnant (*Festuca*) and grown in the greenhouse using sterilized soil in 49-mL Fir Cell Cone-Tainers™ (Steuwe and Sons, Corvallis, OR).

Holcus was removed from all plots using hand tools in December 1999; resprouting plants and new germinants were treated with glyphosate herbicide (Roundup™, Monsanto Corporation, St. Louis, MO) in January 2000. Native grass seedlings were planted between January 17 and February 5, 2000 at densities reflective of their adult sizes: 100, 64, and 49 plants per plot for *Bromus*, *Festuca* and *Calamagrostis*, respectively. Cover types were maintained by hand weeding (planted plots) or annual glyphosate application (bare plots). Plots were sown with *Holcus* seeds in November 2001. In addition, fences were constructed around the plots used in the experiment described here in summer 2000. Fences were meant to exclude burrowing animals, but the

treatment was unsuccessful and soil disturbance was similar across fenced and unfenced plots. Fences were therefore removed in October 2002. At the same time, plots were hand-weeded to remove all vegetation in bare plots and all vegetation other than planted individuals in the other cover types.

In November 2002, four 30 cm-diameter circular subplots were established per plot. Two canopy treatments (shaded vs. unshaded) and two soil treatments (undisturbed vs. mound) were crossed and randomly assigned to each subplot. The method used to create shaded or unshaded conditions varied with cover type. In *Bromus* and bare plots, square shade structures, 35 cm on a side and 50 cm tall, were constructed using a double layer of 1 cm-mesh polypropylene fencing (McMaster-Carr, Los Angeles, CA). A gap at the bottom allowed access to insects and small mammals. In *Festuca* and *Calamagrostis* plots, the plant canopy itself provided substantial shading over the soil surface. To create shaded and unshaded subplots the grass canopy was either left in place with leaves sometimes tied together to get more consistent shading over the subplot, or was pinned back using long wires (unshaded). In all cover types, mound subplots were constructed using soil collected with a bucket auger in each plot, outside of the subplots (two 15 cm by 25 cm cores per plot). Soil was coarse-sieved to 1 cm to homogenize soil texture and large clumps of root material were removed. For each mound, half the collected soil was poured into a cylindrical frame; removing the frame resulted in a mound 30 cm wide, the approximate size of natural gopher mounds in other coastal prairie sites (Peart 1989b; DiVittorio et al. 2007).

Holcus seeds were collected from the surrounding population in August 2002. Subsamples were germinated in the lab to assess the number of viable seeds per mg and calculate the mass needed to obtain 2000 *Holcus* seeds/m² (141/subplot), which is one third of the *Holcus* seed rain measured in native-dominated patches in a heavily invaded coastal prairie site (Peart 1989a). Two days after the first rains in November 2002, seeds were added to all subplots by sprinkling seeds evenly inside a 30 cm-diameter frame; wet conditions prevented movement after seed additions (M. Thomsen personal observation).

To estimate light availability across shading and disturbance treatments, photosynthetically active radiation (PAR) was measured at the soil surface using a hand-held quantum sensor (LI-COR Environmental, Lincoln, NE). Light measurements were taken in the center of each subplot within two hours of solar noon on a single clear day in February 2003. In March and August 2003, soil cores were collected from four randomly selected subplots per cover, mound, and shading combination. A pair of 2 cm by 7.5 cm cores were

collected and combined from each sampled mound, and a single 2 cm by 15 cm core was collected from each undisturbed subplot selected for sampling. All cores were transported on ice and refrigerated prior to extraction. Soils were sieved through a 2 mm mesh and a weighed subsample was dried at 100°C and re-weighed to determine gravimetric percent water content. Approximately 13 g wet soil (10–12 g dry mass) was added to 50 mL 2M KCl and shaken for 45 min. Extracts were filtered through pre-washed Whatman 40 Quantitative Grade Filter Paper (Whatman Group, Middlesex, UK) and frozen until being analyzed for ammonium and nitrate concentration on a Lachat Autoanalyzer (Lachat Instruments, Loveland, CO). Ion concentrations were corrected for molecular weight, percent water content and grams of non-gravel soil per cm² to calculate μg available N per cm² of soil.

In mid May 2003 (end of wet season), all *Holcus* seedlings in the center 100 cm² area of each subplot were counted and marked with a toothpick. Since some seedling mortality could have occurred before this time point, seedling numbers at this time are regarded as an estimate of seedling establishment rather than emergence. Subplots were re-censused in August 2003 (peak dry season) for living *Holcus* seedlings to evaluate patterns of survival across experimental treatments; no new unmarked seedlings were detected at this time point, and living plants at this time point generally were robust.

All statistical analyses were conducted using JMP 10 (SAS Institute, Cary, NC). May and August seedling numbers and N availability data were square root transformed, light availability data were log transformed, and percent water content data were arcsine-square root transformed to meet the assumptions of normality and equality of variances. The mean number of *Holcus* seedlings per plot (averaging across subplots) was determined for May and August, and the effect of cover type on *Holcus* seedling numbers was determined using one-way ANOVA. Analyses of shading and soil treatment effects on seedling numbers were conducted separately for each species because of the different methods used to achieve shaded conditions in bare and *Bromus* as opposed to *Festuca* and *Calamagrostis* plots; a sequential Bonferroni technique (Rice 1989) was used to assure an overall error rate of <0.05 for each outcome variable. Establishment, survival, and light data were analyzed using a randomized complete block ANOVA model (plot as the blocking factor), with shading and disturbance treatments crossed within each plot. Because N and water were sampled in four randomly-selected subplots per treatment combination, the effects of experimental manipulations on those data were analyzed as a randomized incomplete block design. Pairwise differences were evaluated using Tukey tests.
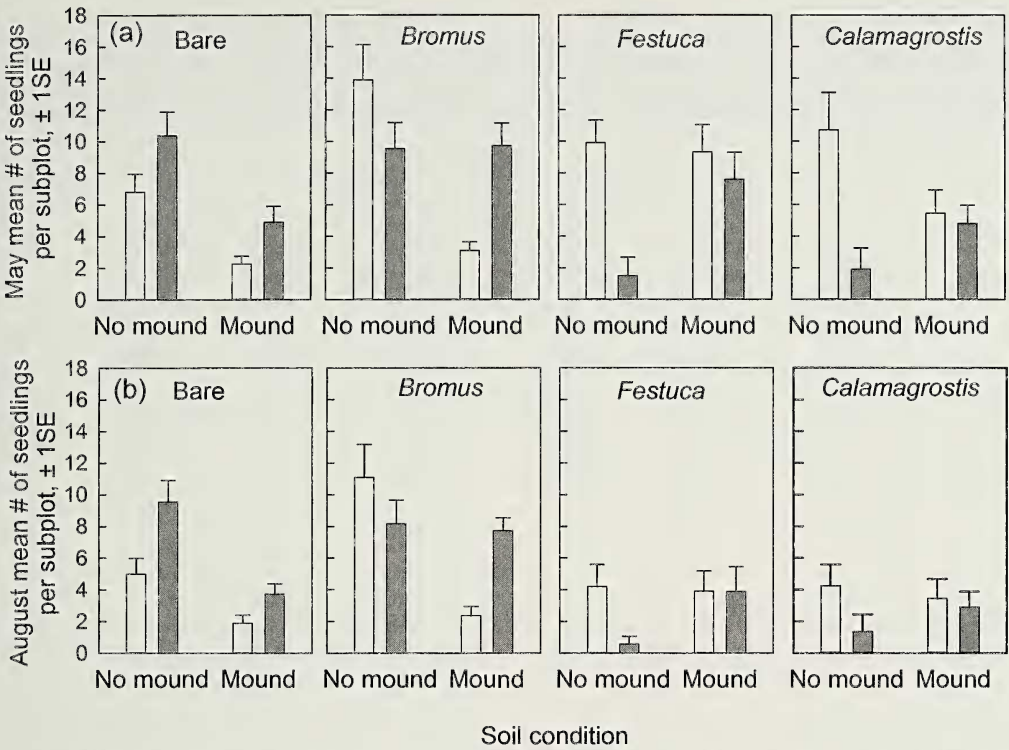
FIG. 1. Establishment of *Holcus* seeds added to subplots in May (a) and the survival of seedlings until August of their first year (b). White bars represent means for unshaded/open canopy subplots and gray bars represent shaded/closed canopy subplots.

RESULTS

Holcus Establishment and Survival

Cover type significantly affected *Holcus* seedling establishment in May ($F_{3,40} = 3.38$, P < 0.05) and survival until August ($F_{3,40} = 9.30$, P < 0.0001). Tukey tests indicated no significant pairwise differences in May seedling numbers across cover types. In August however, there were on average seven surviving *Holcus* seedlings per 100 cm² in *Bromus* plots, significantly more than the three found in *Festuca* and *Calamagrostis* plots. August seedling numbers in bare plots were intermediate.

Within bare plots, shade structures increased *Holcus* seedling establishment in May from an average of 4.5 to 7.6 per 100 cm², and undisturbed areas of bare plots had more than twice as many *Holcus* seedlings as mounds (Fig. 1, Table 1). Shading and disturbance interacted to determine the number of *Holcus* seedlings that established in *Bromus* plots. There were an average of 11 *Holcus* seedlings in *Bromus* undisturbed and shaded mound subplots, more than three times as many as were found on unshaded mounds. Shading and soil disturbance interacted differently in their effects on *Holcus* establishment in *Festuca* and *Calamagrostis* plots. Undisturbed, shaded subplots had an average of

two *Holcus* seedlings per 100 cm², while all other subplots averaged eight *Holcus* seedlings in *Festuca* plots and seven in *Calamagrostis* plots.

The number of *Holcus* seedlings sampled in bare plots in August was significantly affected by canopy condition and soil disturbance (Fig. 1, Table 1). Shade structures nearly doubled the number of *Holcus* survivors in bare plots, to an average of seven seedlings per 100 cm²; mounds decreased the number of seedlings in August by more than one half. Shading and disturbance treatments interacted in their effect on *Holcus* seedling numbers in August in *Bromus* plots. Unshaded *Bromus* mounds had fewer than one-third as many *Holcus* seedlings as the other treatments, which averaged 9.5 seedlings. The number of *Holcus* seedlings sampled in August in *Festuca* and *Calamagrostis* plot types averaged three seedlings per 100 cm² and was not significantly affected by shade manipulation or soil disturbance treatments.

Light, N, and Water Availability

Light at the soil surface was significantly lower inside shade structures constructed in bare and *Bromus* plots, by approximately 60% in bare plots and 90% in *Bromus* plots (Table 1, Fig. 2). In *Bromus* plots, mound creation increased PAR

TABLE 1. RESULTS OF SIGNIFICANCE TESTING FOR THE EFFECT OF EXPERIMENTAL MANIPULATIONS ON *HOLCUS* SEEDLING NUMBERS AND ON PAR AT THE SOIL SURFACE. Data were analyzed separately for each species, and bolded P values indicate significant effects after a sequential Bonferroni technique was applied to assure P < 0.05 for each outcome variable. Canopy refers to shade structures created in bare and *Bromus* plots, and to whether the canopy was left in place or pinned back in *Festuca* and *Calamagrostis* plots. Soil refers to simulated gopher mounds in all plot types.

		# May		#August		PAR	
		$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P
Bare	Canopy	25.98	**<0.0001**	20.98	**<0.0001**	7.6	**<0.01**
	Soil	73.34	**<0.0001**	44.6	**<0.0001**	0.07	0.79
	Canopy*Soil	0.16	0.68	0.48	0.49	2.32	0.14
Bromus	Canopy	1.76	0.19	2.9	0.1	222.15	**<0.0001**
	Soil	10.03	**<0.01**	10.59	**<0.01**	38.29	**<0.0001**
	Canopy*Soil	12.48	**<0.01**	11.23	**<0.01**	2.78	0.11
Festuca	Canopy	23.58	**<0.0001**	5.72	0.23	142.7	**<0.0001**
	Soil	10.69	**<0.01**	4.97	<0.05	7.2	<0.05
	Canopy*Soil	18.59	**<0.001**	4.03	0.05	4.09	0.01
Calamagrostis	Canopy	14.03	**<0.001**	6.45	<0.05	150.7	**<0.0001**
	Soil	0.38	0.5	2.16	0.15	25.89	**<0.0001**
	Canopy*Soil	12.04	**<0.01**	2.12	0.16	0.31	0.58

by 60%. Similarly, PAR in *Festuca* and *Calamagrostis* subplots in which the canopy had been pulled back were approximately 50 and 25 times higher, respectively, than in closed-canopy subplots. Soil disturbance also increased PAR in *Calamagrostis* plots; light availability was approximately four times greater on mounds as compared to undisturbed subplots.

Experimental manipulations had no effect on N availability in March (Table 2, Fig. 3). In August, soil N availability was unaffected by shading and disturbance treatments in bare and *Bromus* plots. August N levels were approximately doubled on *Festuca* mounds relative to undisturbed areas, and nearly three times as great on mounds in *Calamagrostis* plots as compared to undisturbed subplots.

Shading treatment interacted with disturbance in determining March water availability in bare plots, so that undisturbed areas and shaded mounds had similarly higher soil moisture levels, but soil moisture on unshaded mounds was approximately one-third as great (Table 3, Fig. 4). Shading increased March water availability by 38% in *Bromus* plots, 46% in *Festuca* plots, and 27% *Calamagrostis* plots. At the same time, mounds decreased water availability by approximately 50% in *Bromus, Festuca,* and *Calamagrostis* plots. In August, shading increased water availability by 30% in *Bromus* plots, but had no effect on water availability in other cover types. In contrast, mounds significantly decreased water levels by approximately 60% in all plot types.

DISCUSSION

As we predicted, the effects of shading and disturbance treatments depended on resident identity. *Holcus* establishment was generally increased by shade structures in bare and *Bromus* plots. The open conditions in these plot types likely increase summertime water deficits, so the positive effect of reduced water stress inside
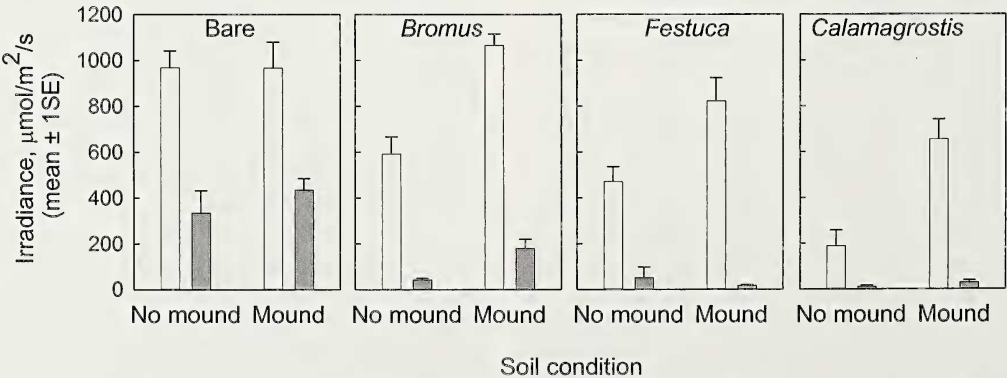

FIG. 2. Availability of photosynthetically active radiation at the soil surface in experimental subplots. White bars represent means for unshaded/open canopy subplots and gray bars represent shaded/closed canopy subplots.

TABLE 2.   RESULTS OF SIGNIFICANCE TESTING FOR THE EFFECT OF EXPERIMENTAL MANIPULATIONS ON MARCH AND AUGUST NITROGEN AVAILABILITY. Data were analyzed separately for each species; bolded P values indicate significant effects after a sequential Bonferroni adjustment was applied to assure an overall P < 0.05 for each month. Canopy refers to shade structures created in bare and *Bromus* plots, and to whether the canopy was left in place or pinned back in *Festuca* and *Calamagrostis* plots. Soil refers to simulated gopher mounds in all plot types.

		March N		August N	
			P		P
Bare	Canopy	$F_{1,11.9} = 1.38$	0.26	$F_{1,11.2} = 8.31$	0.01
	Soil	$F_{1,12} = 0.70$	0.42	$F_{1,11.3} = 11.29$	0.01
	Canopy*Soil	$F_{1,11.9} = 0.03$	0.87	$F_{1,11.2} = 1.82$	0.2
Bromus	Canopy	$F_{1,9.4} = 9.38$	0.02	$F_{1,11.6} = 1.61$	0.23
	Soil	$F_{1,9.7} = 7.95$	0.01	$F_{1,7.0} = 7.89$	0.03
	Canopy*Soil	$F_{1,9.5} = 4.19$	0.07	$F_{1,10.8} = .33$	0.57
Festuca	Canopy	$F_{1,12} = 8.31$	0.58	$F_{1,10.1} = 6.97$	0.02
	Soil	$F_{1,12} = 0.50$	0.01	$F_{1,11.9} = 55.38$	**<0.0001**
	Canopy*Soil	$F_{1,12} = 0.31$	0.49	$F_{1,10.1} = 3.64$	0.09
Calamagrostis	Canopy	$F_{1,11.1} = 2.5$	0.14	$F_{1,12.0} = 0.11$	0.7
	Soil	$F_{1,11.1} = 1.05$	0.33	$F_{1,12.0} = 25.26$	**<0.001**
	Canopy*Soil	$F_{1,10.04} = 0.31$	0.59	$F_{1,12.0} = 0.06$	0.8

the shade structures may have outweighed the negative effect of decreased light availability. Shade structures may have also functioned as wind shelters, which have been shown to affect plant performance at BMR (Lortie and Cushman 2007). In contrast, increased light availability in *Festuca* and *Calamagrostis* subplots in which the canopy had been pulled back increased *Holcus* establishment, despite lower water availability. Management actions such as mowing, grazing, and burning, which will increase light penetration to the soil surface in native bunchgrass stands, should be carefully evaluated in terms of their potential to create opportunities for *Holcus* establishment.

The effects of soil disturbance also differed between bare and *Bromus* vs. *Festuca* and *Calamagrostis* plots. Mounds decreased *Holcus* establishment and survival in bare subplots and unshaded *Bromus* subplots, as might be expected given the open, harsh nature of the treatments.
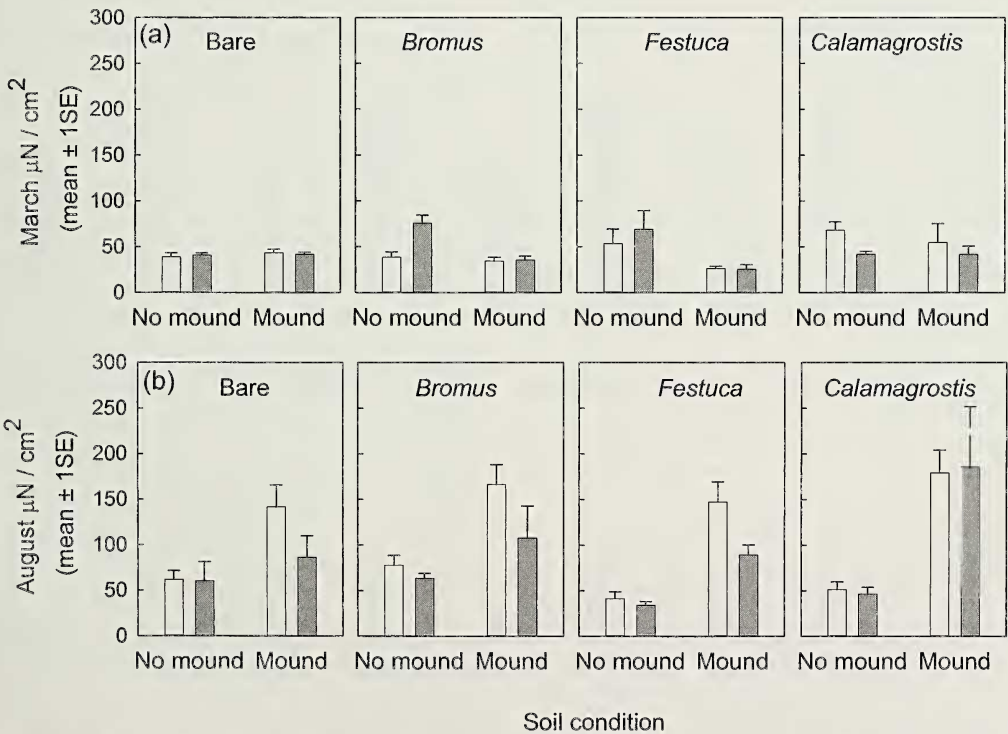

FIG. 3.   Nitrogen availability in experimental subplots in March (a) and August (b). White bars represent means for unshaded/open canopy subplots and gray bars represent shaded/closed canopy subplots.

TABLE 3. RESULTS OF SIGNIFICANCE TESTING FOR THE EFFECT OF EXPERIMENTAL MANIPULATIONS ON MARCH AND AUGUST WATER AVAILABILITY. Data were analyzed separately for each species; bolded p values indicate significant effects after a sequential Bonferroni adjustment was applied to assure an overall P < 0.05 for each month. Canopy refers to shade structures created in bare and *Bromus* plots, and to whether the canopy was left in place or pinned back in *Festuca* and *Calamagrostis* plots. Soil refers to simulated gopher mounds in all plot types.

		March water		August water	
			P		P
Bare	Canopy	$F_{1,11.0} = 27.48$	**<0.001**	$F_{1,10.7} = 0.12$	0.74
	Soil	$F_{1,9.8} = 62.53$	**<0.0001**	$F_{1,10.97} = 88.98$	**<0.0001**
	Canopy*Soil	$F_{1,11.04} = 18.90$	**<0.0001**	$F_{1,10.7} = 1.14$	0.31
Bromus	Canopy	$F_{1,10.0} = 15.50$	**<0.01**	$F_{1,12.0} = 37.97$	**<0.0001**
	Soil	$F_{1,8.2} = 88.97$	**<0.0001**	$F_{1,9.0} = 180.09$	**<0.0001**
	Canopy*Soil	$F_{1,9.0} = 5.42$	0.05	$F_{1,11.3} = 3.26$	0.09
Festuca	Canopy	$F_{1,9.8} = 10.12$	**<0.01**	$F_{1,6.5} = 8.18$	0.26
	Soil	$F_{1,11.8} = 26.6$	**<0.001**	$F_{1,11.9} = 188.50$	**<0.0001**
	Canopy*Soil	$F_{1,9.8} = 2.8$	0.12	$F_{1,6.5} = 3.07$	0.13
Calamagrostis	Canopy	$F_{1,11.5} = 13.36$	**<0.01**	$F_{1,10.9} = 4.05$	0.07
	Soil	$F_{1,11.5} = 78.95$	**<0.0001**	$F_{1,10.9} = 99.28$	**<0.0001**
	Canopy*Soil	$F_{1,9.9} = 2.47$	0.15	$F_{1,9.1} = 0.14$	0.02

The lower water availability on mounds in bare and *Bromus* plots may explain this pattern. We found no effect of a watering treatment on *Holcus* invasion in our earlier work at the BMR (Thomsen and D'Antonio 2007), but this work did not involve gopher mounds. Also, *Holcus* invasion was facilitated by water addition in a more interior and drier prairie site (Thomsen et al. 2006b). Mounds increased *Holcus* seedling establishment in shaded *Festuca* and *Calamagrostis* subplots. The result is difficult to explain, since resource availability was either similar between mound and undisturbed shaded areas (light and March N levels) or lower on mounds (March water availability). It is possible that the soil disturbance directly affected *Holcus* seed germination, resulting in higher rates of seedling establishment.
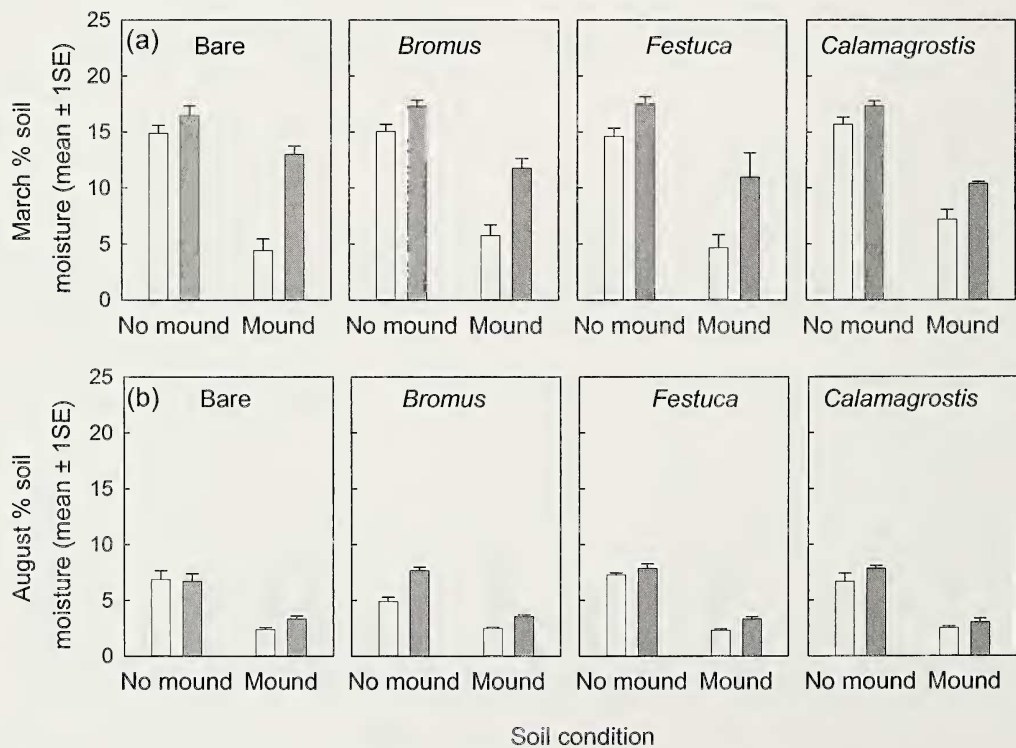

FIG. 4. Water availability in experimental subplots in March (a) and August (b). White bars represent means for unshaded/open canopy subplots and gray bars represent shaded/closed canopy subplots.

Other researchers have found that gopher mounds increase N availability relative to undisturbed areas in California grasslands (Canals et al. 2003; Eviner and Chapin 2005); similarly, we detected higher N availability on mounds in *Festuca* and *Calamagrostis* plots in August. Given the low water availability on mounds in August, however, *Holcus* seedlings are unlikely to benefit from increased nutrient availability at that time. In a greenhouse study, we found that *Holcus* was a dominant competitor against native and exotic perennial grass seedlings, regardless of N level (Thomsen et al. 2006a). Thus, even if mound creation increases N availability at times not sampled here, it may not strongly affect *Holcus* performance relative to native species.

Overall, the results of this experiment do not support the hypothesis that small-scale disturbances created by fossorial mammals are a dominant factor in promoting the invasion of California coastal prairie by *Holcus lanatus*. Open canopy microsites and soil disturbance decreased *Holcus* seedling numbers in bare and *Bromus* plots, and had no effect on *Holcus* survival over summer in *Festuca* and *Calamagrostis* plots. Instead, the highest overall number of *Holcus* seedlings in August was documented in undisturbed *Bromus* plots. Thus, low competitive resistance from certain species provides *Holcus* with better conditions for establishment than those found on mounds. *Bromus* may even facilitate *Holcus* establishment through mild shading with insignificant competition, or through another unidentified mechanism. The relatively high establishment and survival we found in bare plots further suggests that larger-scale disturbances, such as those created by badgers or feral pigs, could promote *Holcus* invasion in coastal prairie (Kotanen 2004). Cushman et al. (2004) found that pig disturbance decreased the biomass of mature exotic perennial grasses in a coastal prairie site, but seedling establishment data were not reported.

Two other studies have examined *Holcus* colonization of gopher mounds in California coastal prairie, with somewhat contrasting results. DiVittorio et al. (2007) found that *Holcus* seedlings were second only to *Aira caryophylla* L. in their abundance on experimental gopher mounds in a coastal prairie site near the BMR. Their measurements were taken in May, which is also when we detected high numbers of *Holcus* seedlings mounds in *Festuca* and *Calamagrostis* subplots; longer-term seedling survival was not monitored. Peart (1989b) added *Holcus* seeds to natural gopher mounds in coastal prairie patches dominated by exotic annual grasses and found that, relative to undisturbed areas, mounds increased *Holcus* survival and seed production during the first year of growth. The contrast

between our results and those of Peart (1989b) could be the result of weaker competition from annual grasses (as opposed to native perennials in our study), or annual- or site-level climatic variation; a cooler summer or an overall wetter site could have ameliorated the water stress experienced by seedlings on mounds. The higher seed density (80,000 per m^2) used by Peart (1989b) may also have contributed to the higher levels of *Holcus* seedling establishment seen on mounds in that study. Here, the seed density (2000 per m^2) was chosen to mimic *Holcus* seed dispersal from invaded areas into native grass-dominated patches, and is similar in magnitude to the 3856 *Holcus* seeds/m^2 measured by DiVittorio et al. (2007) across grassland plots averaging 30% relative cover of *Holcus*. DiVittorio et al. (2007) found that exotic plant dominance on mounds was positively correlated with propagule supply of exotic species, in keeping with the prediction that high propagule supply can overcome both biotic (e.g., competition) and abiotic (e.g., water deficit) forms of resistance to invasion (D'Antonio et al. 2001).

CONCLUSIONS

The combined results of this study and of Thomsen and D'Antonio (2007) highlight how patterns of invasive plant establishment vary across the landscape. Here, we found that invader establishment and the net effect of disturbance on invasion depends on resident identity. In Thomsen and D'Antonio (2007) we documented the same pattern of *Holcus* seedling establishment across native plot types, and further illustrated how native species differences also affected the influence of underlying variation in environmental conditions. *Holcus* seedlings in *Bromus* plots benefited due to the better abiotic conditions found lower on a hillslope, but in *Calamagrostis* plots, the low areas with beneficial conditions were protected by competitive residents (Thomsen and D'Antonio 2007). Accounting for natural variation in the potential for invasive plant establishment across the landscape will allow us to fine-tune management strategies and more successfully decrease the abundance and spread of invasive species.

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